Received 30 March 2005; revised and accepted 17 May 2005

Habitat associations of an Odonata community in a lower montane rainforest in Papua New Guinea

Steffen Oppel

Wildlife Conservation Society, PO Box 277, Goroka, EHP, Papua New Guinea.
<steffen.oppel@gmx.net>
present address: Department of Biology and Wildlife, 211 Irving 1, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

Key words: Odonata, dragonfly, dragonfly assemblage, habitat association, ordination, canonical correspondence analysis, Papua New Guinea.

Abstract

I sampled odonates in pristine lower montane rainforest in Papua New Guinea over several months, recording habitat characteristics for all encounters with adult odonates. Using ordination techniques such as cluster analysis and canonical correspondence analysis I then classified the odonate fauna into assemblages correlated with environmental factors. Within the 2.5 km^2 study area I found 61 species and a very high ratio of Zygoptera vs Anisoptera. Cluster analysis identified seven distinct assemblages associated with permanent rivers and creeks, temporary streams, puddles, or permanent standing water. Shading, water speed and water permanence were important factors distinguishing the assemblages. Anisoptera were absent from three habitats in the forest interior with temporary water sources. Species associated with temporary water sources and other microhabitats in the forest interior are presumed to be reliant on the high and aseasonal rainfall and the humid conditions of the rainforest. These species are likely to be very intolerant towards deforestation or other disturbance, and should be regarded as indicators for intact rainforest ecosystems. 40% of all species were considered as rare, and local endemism might be high, further stressing the importance of intact rainforest for the survival of many species of Odonata.

Introduction

Many species of Odonata are confined to specific habitats both during larval and adult life stages (Corbet 1999: 9; De et al. 1999; Korkeamäki & Suhonen 2002; Watanabe et al. 2004). Species with similar habitat preferences can be grouped to form distinct assemblages characteristic of particular habitats (Ormerod & Edwards 1987; Schridde & Suhling 1994; Osborn & Samways 1996; Stewart & Samways 1998; Clausnitzer 2003; Schindler et al. 2003). In tropical rainforests the structural complexity of the habitat and concomitant large variety of water sources

provides habitat for many different odonate species, and this is especially so in montane areas with a wide range of aquatic microhabitats (Furtado 1969; Vick 1999, 2002; Dijkstra & Lempert 2003). Papua New Guinea (PNG) is known for its very high biodiversity in many groups, probably owing to a rugged mountainous landscape that enhances local endemism (Lieftinck 1942, 1949; Heads 2001, 2002). The odonate fauna of PNG is poorly studied and distribution and habitat requirements of many species are unknown (Brooks & Richards 1992; Polhemus 1995; Mack 1998; Rowe 2004).

In this study I sampled odonates for several months in an aseasonal lower montane rainforest in PNG, and recorded habitat variables for all encounters. I then used ordination techniques to classify the odonate assemblage along a set of environmental gradients. The resulting analysis provides an overview of distinct odonate assemblages and their habitats. This knowledge will enable the identification of species and assemblages that are vulnerable to habitat modification, and thus will help to define conservation priorities for certain habitat types.

Material and methods

Study location

The study site was located on the southern scarp of the central mountain range of Papua New Guinea (6°43'S, 145°05'E) and covered ca 2.5 km^2 between 850 m to 1,300 m a.s.l. It was situated within a 2,800 km^2 tract of continuous primary rainforest, with a very high plant diversity (Wright et al. 1997). Rainfall at the site was high and aseasonal, with ca 6,500 mm per annum (Wright et al. 1997). Small depressions on the forest floor filled with water during heavy rains and formed temporary puddles that dried up within three days of no rain. The study area included one small (0.25 ha), fish-free pond, as well as innumerable streams and creeks with a high variability of flow rate, depending on rainfall. Forest temperature ranged from 18°C to 26°C, but open areas in rivers exposed to longer periods of sun were much warmer. The region was very sparsely populated, and the nearest villages sustaining a small population of hunters and subsistence gardeners were 10 km away. A moratorium on hunting and tree cutting over the entire study area had been in place since 1989, and the study area could be regarded as pristine tropical rainforest.

Sampling methods

Odonates were sampled between December 2003 and August 2004, with intensive sampling periods in February, April, and July 2004. Habitat variables were recorded at every site where an adult odonate was observed. In order to reduce autocorrelation between habitat records of a given species, habitat samples were only taken from localities spaced at least 20 m apart. Unknown or unidentifiable species were collected and preserved as specimens, and later examined and identified by John Michalski and Nick Donnelly. Not all specimens could be identified to species level, and some species were new to science and have yet to be formally described.

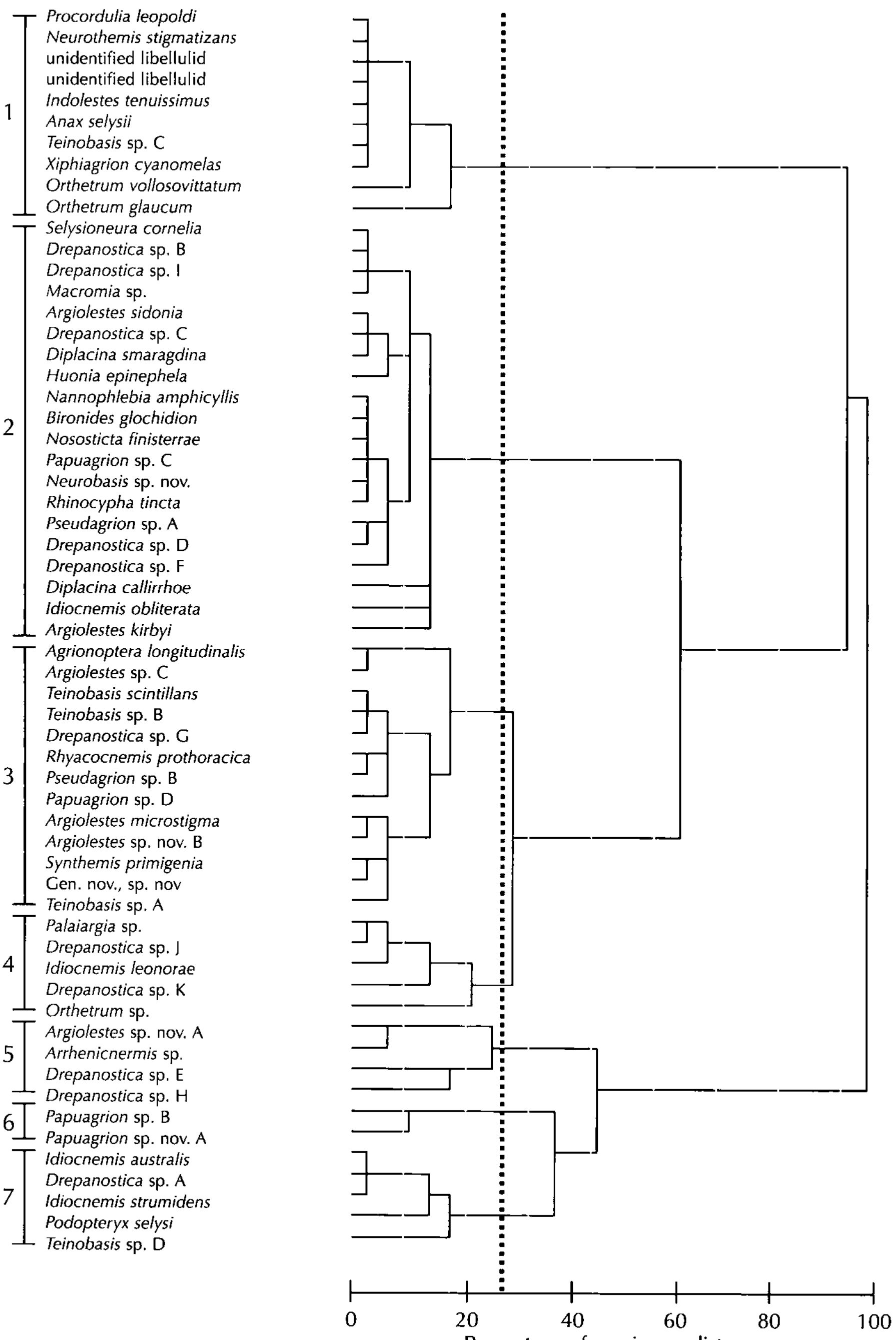

Figure 1: Dendrogram of a hierarchical cluster analysis linking the odonate species of a lower montane rainforest in Papua New Guinea according to habitat variables. — The dashed vertical line indicates the 25% cut-off of the maximum squared Euclidean distance used to determine clusters. Cluster number is indicated on the left.

Table 1. List of all species recorded at Crater Mountain Biological Research Station, Papua New Guinea, in 2004, including their habitat cluster membership and abundance. For cluster information refer to Table 2, for abundance categories see text. Note that habitat information given for 'rare' species is based on very few observations and therefore needs to be viewed with caution.

Species	Habitat	Cluster	Abundance
Calopterygidae			
Neurobasis sp. nov.	River	2	Abundant
Chlorocyphidae			
Rhinocypha tincta Rambur	River	2	Common
Lestidae			
Indolestes tenuissimus (Tillyard)	Pond	1	Abundant
Megapodagrionidae			
Argiolestes kirbyi (Förster)	River	2	Common
microstigma Lieftinck	Creek	3	Common
sidonia Martin	River	2	Common
sp. nov. A	Temporary stream, steep	5	Rare
sp. nov. B	Temporary stream	3	Rare
sp. C	Temporary stream	3	Uncommon
sp. D	No data	-	Uncommon
Podopteryx selysi (Förster)	Forest/mud puddle	7	Uncommon
Coenagrionidae			
Palaiargia sp.	Creek	4	Rare
Papuagrion sp. nov. A	Forest/sunny patch	6	Uncommon
sp. B	Forest/sunny patch	6	Uncommon
sp. C	River	2	Rare
sp. D	Temporary stream	3	Rare
Pseudagrion sp. A	River	2	Rare
sp. B	Temporary stream	3	Rare
Teinobasis scintillans Lieftinck	Temporary stream	3	Uncommon
sp. A	Temporary stream	3	Rare
sp. B	Temporary stream	3	Common
sp. C	Pond	1	Rare
sp. D	Forest/mud puddle	7	Rare
Xiphiagrion cyanomelas Selys	Pond	1	Abundant
Isostictidae			
Selysioneura cornelia Lieftinck	River	2	Uncommon
sp.	No data	-	Rare
Platycnemidae			
Arrhenicnemis sp.	Temporary stream, steep	5	Rare
Idiocnemis australis Gassmann	Forest/mud puddle	7	Uncommon
leonorae Lieftinck	Creek	4	Uncommon
obliterata Lieftinck	River	2	Uncommon
strumidens Lieftinck	Forest/mud puddle	7	Common
Rhyacocnemis prothoracica Lieftinck	Temporary stream	3	Abundant
Gen. nov., sp. nov.	Temporary stream	3	Rare

Species	Habitat	Cluster	Abundance
Platystictidae			
Drepanosticta sp. A	Forest/mud puddle	7	Uncommon
sp. B	River	2	Rare
sp. C	River	2	Rare
sp. D	River	2	Rare
sp. E	Temporary stream, steep	5	Rare
sp. F	River	2	Common
sp. G	Temporary stream	3	Uncommon
sp. H	Temporary stream, steep	5	Uncommon
sp. I	River	2	Common
sp. J	Creek	4	Rare
sp. K	Creek	4	Uncommon
Protoneuridae			
Nososticta finisterrae (Förster)	River	2	Abundant
Aeshnidae			
Anax selysii Förster	Pond	1	Abundant
Corduliidae			
Procordulia leopoldi Fraser	Pond	1	Rare
Macromia sp.	River	2	Common
Synthemistidae			
Synthemis primigenia Förster	Temporary stream	3	Uncommon
Libellulidae			
Agrionoptera longitudinalis Selys	Temporary stream	3	Rare
Bironides glochidion Lieftinck	River	2	Rare
Diplacina callirrhoe Lieftinck	River	2	Uncommon
smaragdina Selys	River	2	Rare
Huonia epinephela Förster	River	2	Abundant
Nannophlebia amphicyllis Lieftinck	River	2	Common
Neurothemis stigmatizans (Fabricius)	Pond	1	Uncommon
Orthetrum glaucum (Brauer)	Pond	1	Common
sp.	Creek	4	Rare
villosovittatum (Brauer)	Pond	1	Abundant
unidentified libellulid A	Pond	1	Rare
unidentified libellulid B	Pond	1	Rare

The following habitat variables were recorded at every point where an adult odonate was observed: stream order (1: small headwater stream to 5: big river); water speed (0: 0 m s-1, 1: 0.01-0.3 m s-1, 2: 0.31-0.5 m s-1, 3: 0.51-1 m s-1, 4: > 1 m s-1); width of water source (m); nature of water body (permanent or temporary, lotic or lentic); shading (% of water body); substrate (mud, sand, gravel, rock); presence of boulders > 1 m (Y/N); presence of standing pools (Y/N); presence of temporarily submerged banks (Y/N); presence of water-filled tree-holes or *Pandanus* sp. trees (Y/N); % moss cover of hard substrates; vegetation debris (% cover of water source); presence of floating vegetation (Y/N); and distance to the nearest sunny patch (m).

Table 2. Position of centroids of species clusters in relation to environmental variables for seven odonate assemblages from a lower montane rainforest in Papua New Guinea; for membership of species see Table 1.

Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Number of species							
	10	20	13	5	4	2	5
Class							
	Pond	River	Stream	Creek	Stream	No water	Puddle
Water speed							
	0	> 1 m/s	0.3 m/s	0.7 m/s	0.1 m/s	0	0
Nature of water source							
	Permanent Standing	Permanent Running	Temporary Running	Permanent Running	Temporary Running	None No Water	Temporary Standing
% shading							
	42	58	88	64	86	68	79
Substrate							
	Mud	Gravel	Mud	Sand	Sand	Mud	Mud
Boulder							
	No	Yes	No	No	No	No	No
Pools							
	Yes	Yes	Yes	Yes	No	No	No
Floating vegetation							
	Yes	No	No	No	No	No	No
Mean distance to sun [m]							
	0.0	2.0	7.8	3.6	11.4	0.0	6.2

Analyses

Species abundances were classified into four categories, rare (1-5 individuals), uncommon (6-20), common (21-100), and abundant (> 100). The habitat variables were used to classify the odonate assemblage into several groups, constituting distinct communities for each habitat type. Species with several habitat records were classified by the mean and modal values of metric or ordinal variables, respectively. I transformed all variables to a uniform scale to account for differences in scaling units (McGarigal et al. 2000), and then used a hierarchical cluster analysis, and a cut-off value of 25% of the maximum squared Euclidean distance to group species into clusters with similar environmental characteristics (Baptista et al. 2001). The calculations were run with SPSS™ (Norusis 2000). I used the squared Euclidean distance and between-groups linkage as distance measure and linkage rule, respectively.

For analysing the relationship between all environmental variables and species occurrence, a canonical correspondence analysis (CCA, ter Braak 1986) was performed using CANOCO 4.5 (ter Braak & Smilauer 2002). The forward selection mode was chosen to determine the variables explaining most of the variation in the data set, and insignificant variables were eliminated from the final model. A Monte Carlo simulation with 500 permutations was run to test for the significance of the

canonical axes. Assigning each species to one of the clusters I then qualitatively examined the location of clusters along the environmental gradients, and the main variables separating clusters along the canonical axes (Baptista et al. 2001; Schindler et al. 2003).

RESULTS

A total of 61 species (16 Anisoptera, 45 Zygoptera) in 13 families was recorded during the study period, and 418 data points with species and habitat information were obtained. A list of all species and their abundance is presented in Table 1. Most species occurred in small numbers, and 25 species (41%) were classified as rare. Seventeen species (28%) were uncommon, 11 species (18%) were common and eight species (13%) were abundant. Only 59 species were included in cluster analysis and CCA, as no habitat information existed for the remaining two species. The hierarchical cluster analysis identified seven ecologically significant groups with less than 25% of the maximum distance between members of each group (Fig. 1). The position of cluster centroids in relation to environmental variables is presented in Table 2. Two clusters existed for permanent running water sources, with one centred on rivers (fewer shade, coarser substrate with large boulders) and one on creeks (sandy substrate, no boulders, more shade). Another two clusters were identified for temporary streams, and these were mainly separated by gradient and associated differences in substrate and the presence of pools. The remaining three habitats classified by cluster analysis were the pond, temporary puddles and sunny clearings in the forest interior. No species occurred in more than two of the habitats as defined above.

The group including species associated with rivers contained the highest number of species (20), followed by the assemblage of smaller and shadier creeks with 13 species. Anisopterans occurred only in four of the assemblages, and all but two species were absent from all temporary water sources (clusters 5-7). The sunniest habitats (pond and river) hosted the largest number of Anisoptera species (7 and 6, respectively), and the pond was the only habitat where more Anisoptera occurred than Zygoptera. Two Anisoptera species, *Synthemis primigenia* and *Agrionoptera longitudinalis*, were found in the forest interior along temporary streams that left small puddles behind. A female *S. primigenia* was observed to oviposit into this microhabitat.

The most common species in rivers were *Huonia epinephela*, *Diplacina callirrhoe*, *Neurobasis* sp. nov., *Nososticta finisterrae*, *Argiolestes kirbyi* and *A. sidonia*. The latter four occurred along narrower or shadier sections and were sometimes found in smaller creeks, or – in the case of teneral *A. sidonia* – well away from any running water source in the forest. *Idiocnemis leonorae* was the most common representative of small permanent creeks. The fish-free pond hosted the highest odonate population density in the study area. On sunny days up to 100 individuals mostly of *Procordulia leopoldi*, *Anax selysii*, *Orthetrum villosovittatum*, and *Xiphiagrion cyanomelas* were flying over the water surface or along the banks. Two species, a *Teinobasis* sp. and *Indolestes tenuissimus*, were generally found in the same microhabitat of bank vegetation, but were almost never observed on the same day. Six of the 10 pond species were found in no other location other than this pond.

Table 4. Correlations of environmental factors with the four axes of the Canonical Correspondence Analysis ordinating the odonate community in a lower montane rainforest in Papua New Guinea in 2004. Significance of factors derived from Monte Carlo permutation tests, *: $p < 0.05$, **: $p < 0.01$.

Factor	Axis 1	Axis 2	Axis 3	Axis 4
Water speed **	-0.610	-0.633	-0.193	-0.093
Temporal persistence **	-0.174	-0.670	-0.042	-0.440
Nature of water source **	-0.446	-0.254	-0.004	-0.647
Shade **	-0.008	0.596	-0.087	-0.081
Presence of sandbanks **	-0.284	0.172	-0.150	-0.362
Presence of boulders **	-0.598	-0.686	-0.096	-0.088
Presence of pools **	-0.027	-0.405	-0.579	-0.605
Moss cover *	-0.190	0.354	0.009	-0.419
Floating vegetation **	0.662	-0.278	0.260	-0.307
Distance to sunny patch	-0.082	0.440	0.312	-0.159

Some species were never observed in the vicinity of permanent water sources. Two *Papuagrion* spp. occurred almost exclusively in sunny clearings in the forest, of which *P.* sp. B was the more common. Another group of species was associated with puddles forming temporarily after heavy or persistent rain, and *Idiocnemis strumidens* and *I. australis* were the most common odonates in this habitat. There was some overlap between this assemblage and the one associated with temporary streams that left puddles behind when drying out. *Argiolestes microstigma*, *Rhyacocnemis prothoracica*, and *Teinobasis scintillans* were the most common representatives of the temporary muddy creeks. On steeper slopes, temporary creeks with a sandy substrate did not leave puddles as they dried up, and a different odonate assemblage was found in these creeks. A new and undescribed species of *Argiolestes* and a *Drepanosticta* sp. were the most numerous species in this habitat.

CCA resulted in four axes explaining 97.5% of the environmental variation among species. Species environment correlations were high for the first two axes (Table 3), and both the first axis ($F = 39.92$, $p < 0.01$) and all canonical axes together were significant ($F = 10.72$, $p < 0.01$). Water speed and the presence of boulders exerted the strongest influence on axes 1 and 2. Axis 1 was also strongly influenced by floating vegetation, whereas shade and temporal persistence defined axis 2 (Table 4). The remaining two axes explained the variation caused by the presence of pools (axis 3 and 4), the nature of the water source and moss cover (axis 4). Water speed, temporal persistence, and the presence of pools were the most influential variables in CCA, whereas substrate, stream order and habitat type were eliminated by the forward selection process.

An ordination plot of the first two axes yielded several distinct clusters centred along major gradients, and these were mostly consistent with the groupings of the cluster analysis (Fig. 2). The highest level of overlap existed between the two clusters representing permanent creek species, and the three clusters including temporary stream and puddle species.

Discussion

The odonate community of the studied tropical rainforest site in PNG is species-rich. Given the small area of the study site, the number of species found is high compared with studies of much larger regions in Africa (Samways 1989; Clausnitzer 1999; Vick 1999, 2002; Dijkstra & Lempert 2003) and the Neotropics (Novelo Gutierrez et al. 1988; de Marmels 1998; Ramírez et al. 2000; Paulson 2002). The species richness is also higher than in lowland sites of PNG (Polhemus 1995; Mack 1998), lending some support to Vick's (2002) theory that montane areas may host a larger number of species due to the variety of running water systems. About 40% of all species can be regarded as rare, and local endemism might be very high, as is known for South East Asia (Orr 2003, 2004). Further research is required to determine the species limits (e.g. *Drepanosticta* spp.) and geographic ranges of many Papuan odonates in order to assess the level of endemism.

The ratio of Zygoptera vs Anisoptera found in the study area is also very high compared with studies from other regions (Lieftinck 1976; Novelo Gutierrez et al. 1988; Samways 1989; Khaliq et al. 1992; Osborn & Samways 1996; Stewart & Samways 1998; Ramírez et al. 2000; Orr 2001). This might be due to the pristine and closed nature of the rainforest, which supports a large variety of Zygoptera, but fails to provide habitat suitable for the elevated thermal requirements of most Anisoptera. Only two species of Anisoptera were found in the forest interior. This study thus confirms previous findings that a high β-diversity, as well as a high ratio of Zygoptera vs Anisoptera is an indication for landscapes with little human disturbance (Stewart & Samways 1998; Clausnitzer 2003).

Specific odonate assemblages reflected the considerable variation in size, temporal persistence, water speed and substrate among the water sources found in the study area. Seven distinct assemblages were identified within the study area, with three being associated with standing or no water, and four being associated with running waters of increasing size. A succession of distinct odonate communities along a stream gradient from its source to higher order rivers is consistent with findings of other studies (Legrand & Couturier 1985; Clausnitzer 2003; Dijkstra & Lempert 2003). Differential ability to cope with desiccation and predator avoidance ability of larvae might limit species to certain parts of the river continuum gradient from temporary to permanent running waters (Stoks & McPeek 2003; Johansson & Suhling 2004).

Generally, species richness is considered to increase with stream size and canopy openness (Kinvig & Samways 2000; Clausnitzer 2003; Dijkstra & Lempert 2003). The most species-rich assemblage in this study was the one associated with rivers. Since several species (e.g. *Huonia epinephela*, *Neurobasis* sp. nov., *Diplacina* spp.) ventured up smaller rivers the cluster analysis was not powerful enough to separate two distinct assemblages between large, sunny rivers, and small rivers with a mosaic of sunny and shady stretches, as has been found in other tropical regions (Dijkstra & Lempert 2003). The latter generally had a higher abundance and diversity of odonates, which is consistent with the results of Dijkstra & Lempert (2003) from Guinea. The relatively small number of anisopterans (6) found in the sunny rivers suggests that the local odonate fauna might be depauperate of large, heliophilic Anisoptera usually occurring under sunny and open conditions (Stewart & Samways 1998; Clausnitzer 2003). The absence of a large variety of anisopterans,

especially of the family Gomphidae, is also noteworthy in a biogeographical context. While Australia's gomphid fauna is species-rich (Watson et al. 1991), only one species is known from New Guinea and none was found in this study. Furthermore, only few corduliids and crepuscular species were found in this study, but this might have been due to the relatively small sampling effort at dusk, since other sites in PNG host more crepuscular species (Mack 1998). No effort was made to sample larvae, and it should also be noted that there might have been some sampling unevenness resulting from some Anisoptera being more difficult to capture as adults than most Zygoptera (Corbet 1999: 389).

There was no overlap of species between the permanent creeks and rivers and the small and shady temporary streams. Small streams with little water flow are often filled with leaf litter, and this microhabitat has been found to host a very rich and specific macroinvertebrate fauna in tropical streams (Yule 1996; Bass 2003). The separation of temporary stream dwellers was largely due to different gradient and the resulting difference in substrate and presence of pools. Altogether these two habitats under closed canopy comprised 17 species. This is significantly more than for comparable habitats in Africa, where only few species are found along temporary streams in dense forest (Kinvig & Samways 2000; Clausnitzer 2003). How-

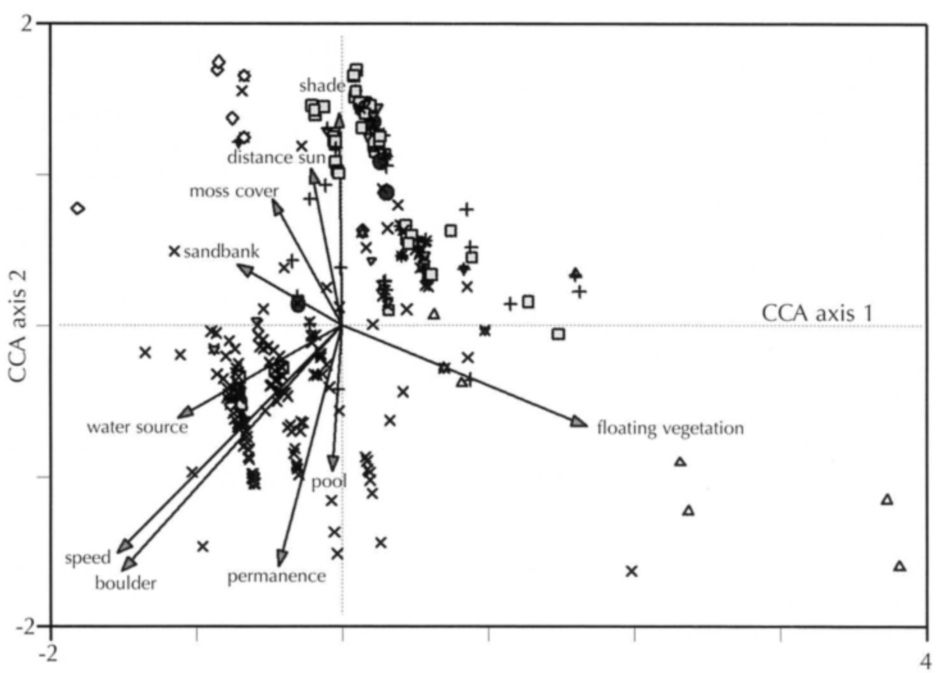

Figure 2: CCA triplot of the canonical axes 1 and 2 in relation to environmental factors of an odonate community in a lower montane rainforest in Papua New Guinea. Symbols represent species data points, assigned to clusters. See Table 2 for definition of cluster environment. — Cluster membership: △ =1, X = 2, ■ = 3, ▼ = 4, ◇ = 5, ● = 6, + = 7.

ever, with *Teinobasis scintillans* and *Argiolestes microstigma* only two representatives of this group were common (> 20 individuals), whereas all other species were uncommon or rare and probably stenotopic. Due to the small sample sizes and the few records for many species there is some uncertainty as to the true abundance and habitat requirements of species considered rare in this study. However, most can probably be regarded as prone to local extinction following habitat modification (Korkeamäki & Suhonen 2002), and it can be assumed that deforestation would gravely endanger their persistence (Clausnitzer 2003).

Two groups were associated with standing water. The first group comprised the species inhabiting the fish-free pond, and most of them were ovipositing into floating macrophytes. The pond was open and sunny, which might explain the proportionally large number of anisopterans (67%) as well as the abundance of common eurytopic species like *Orthetrum villosovittatum*.

Other standing water sources were small temporary puddles in the forest interior, which dried out during periods with little rainfall. In the CCA ordination there was considerable overlap between this group of species and those found either away from any water source or in temporary streams that left puddles as they dried out (Fig. 2). Separation between these groups was probably achieved by canonical axes 3 and 4, i.e. by the presence of pools and the distance to sunny patches.

The most important factor enabling the diverse community associated with small and temporary water sources is probably the aseasonal and abundant rainfall in the study area (Wright et al. 1997). This results in constantly high humidity and soil moisture level, and very low risk of prolonged dry spells. The high rainfall and humidity might also permit species to breed in phytotelmata or water-filled tree holes, as is known from other tropical regions (Lounibos et al. 1987; Fincke 1992, 1994, 1999; Kitching & Orr 1996; Louton et al. 1996; Clausnitzer 1997; Fincke et al. 1997; Yanoviak 2001). These species are found in the forest interior and may comprise the group that is not associated with any surface water source recorded in this study. This assumption is supported by the fact that *Podopteryx selysi*, which was recorded in the forest interior in this study, is known as a phytotelmata specialist (Watson & Dyce 1978; Kitching 2000). Alternatively, some species might have been foraging and utilize a different habitat for reproduction. More research is required to determine the precise habitat requirements of the less known interior forest species.

No species occurred in more than two of the established clusters, which stresses both the heterogeneity of the water systems found in the study area, as well as the narrow ecological amplitude of most rainforest odonates. However, the habitat range of some species might be wider than recorded in this study, and a larger sampling effort might reveal other utilized habitats.

Structuring variables like water hardness, saprobity, conductivity, pH, oxygen content or other factors relating to water chemistry might play an additional role in the habitat selection of odonates, especially in lower order streams (Painter 1999; Baptista et al. 2001; Buss et al. 2002). These variables were not measured in this study, and effects resulting from associations with any of those variables might therefore confound the observed pattern. Human disturbance and pollution of water sources will adversely affect species that have narrow ecological limits with respect to water chemistry (Watson et al. 1982; Brown 1991; Timm et al. 2001). These as well as several species associated with closed forests might therefore assume a role as indicator of ecosystem health (Corbet 1993).

In summary, the odonate assemblages of temporary water sources in the study area in Papua New Guinea are species-rich and probably highly vulnerable due to a high proportion of stenotopic and/or endemic species. Since local endemism is a major criterion for setting conservation priorities (Hill et al. 1995; Willott et al. 2000), and the habitat requirements of most closed forest Zygoptera are unlikely to be met in degenerated forest or in a largely deforested landscape, I propose the use of these groups as indicators of an undisturbed rainforest. An ecosystem-wide approach will be required for their conservation.

Acknowledgements

This study was supported by a grant from the Worldwide Dragonfly Association (WDA), as well as by the International Dragonfly Fund (IDF). I am grateful for the logistical support of the Wildlife Conservation Society, which provided research facilities in Papua New Guinea. The Gimmi and Pawaian people of the Crater Mountain Wildlife Management area were kind enough to host me on their land and were also good companions in the field. The local assistants Joris, Amoli and Oliver greatly improved the number of collected specimens. The Department of Environment and Conservation enabled this study by granting permission to collect and export specimens. John Michalski and Nick Donnelly identified the collected specimens and I greatly appreciate their effort. I would also like to thank Stephen Richards, Bert Orr, and John Michalski for discussions and support, as well as Vincent Kalkman for providing literature. This manuscript was improved by the helpful comments of Bert Orr, John Michalski, and Frank Suhling.

References

Baptista, D.F., L.F.M. Dorville, D.F. Buss & J.L. Nessiamian, 2001. Spatial and temporal organization of aquatic insects assemblages in the longitudinal gradient of a tropical river. Brazilian Journal of Biology 61: 295-304.

Bass, D., 2003. A comparison of freshwater macroinvertebrate communities on small Caribbean islands. Bioscience 53: 1094-1100.

Brooks, S.J. & S.J. Richards, 1992. A new species of *Oreagrion* (Odonata: Coenagrionidae): montane damselflies from New Guinea. Tijdschrift voor Entomologie 135: 141-144.

Brown, K.S., 1991. Conservation of neotropical environments: insects as indicators. In: Thomas, J.A. (ed.) "The conservation of insects and their habitats", Academic Press, London, pp. 349-404.

Buss, D.F., D.F. Baptista, M.P. Silveira, J.L. Nessimian & L.F.M. Dorville, 2002. Influence of water chemistry and environmental degradation on macroinvertebrate assemblages in a river basin in south-east Brazil. Hydrobiologia 481: 125-136.

Clausnitzer, V., 1997. Reproductive behaviour of *Notiothemis robertsi* Fraser (Anisoptera: Libellulidae). Odonatologica 26: 451-457.

Clausnitzer, V., 1999. Dragonfly (Odonata) records of Kakamega Forest, Western Kenya, with notes on the ecology of rain forest species. Journal of East African Natural History 88: 17-24.

Clausnitzer, V., 2003. Dragonfly communities in coastal habitats of Kenya: indication of biotope quality and the need of conservation measures. Biodiversity and Conservation 12: 333-356.

Corbet, P.S., 1993. Are Odonata useful as bioindicators? Libellula 12: 91-102.
Corbet, P.S., 1999. Dragonflies: behavior and ecology of Odonata. Harley Books, Colchester.
De, M.J.P., A.O. Latini & A.P. Reis, 1999. Environmental determination of dragonfly assemblage in aquaculture ponds. Aquaculture Research 30: 357-364.
de Marmels, J., 1998. A five year survey of an odonate community inhabiting a North Venezuelan mountain stream. Odonatologica 27: 189-199.
Dijkstra, K.-D.B. & J. Lempert, 2003. Odonate assemblages of running waters in the Upper Guinean forest. Archiv für Hydrobiologie 157: 397-412.
Fincke, O.M., 1992. Interspecific competition for tree holes: consequences for mating systems and coexistence in neotropical damselflies. American Naturalist 139: 80-101.
Fincke, O.M., 1994. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. Oecologia 100: 118-127.
Fincke, O.M., 1999. Organization of predator assemblages in neotropical tree holes: effects of abiotic factors and priority. Ecological Entomology 24: 13-23.
Fincke, O.M., S.P. Yanoviak & R.D. Hanschu, 1997. Predation by odonates depresses mosquito abundance in water-filled tree holes in Panama. Oecologia 112: 244-253.
Furtado, J.I., 1969. Ecology of Malaysian odonates: biotope and association of species. Verhandlungen Internationaler Verein für Limnologie 17: 863-887.
Heads, M., 2001. Birds of paradise, biogeography and ecology in New Guinea: a review. Journal of Biogeography 28: 893-927.
Heads, M., 2002. Birds of paradise, vicariance biogeography and terrane tectonics in New Guinea. Journal of Biogeography 29: 1-23.
Hill, J.K., K.C. Hamer, L.A. Lace & W.M.T. Banham, 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. Journal of Applied Ecology 32: 754-760.
Johansson, F. & F. Suhling, 2004. Behaviour and growth of dragonfly larvae along a permanent to temporary water habitat gradient. Ecological Entomology 29: 196-202.
Khaliq, A., A. Hayat & A. Hussain, 1992. Some dragonflies of district Mansehra (NWFP). Pakistan Journal of Forestry 42: 74-77.
Kinvig, R.G. & M.J. Samways, 2000. Conserving dragonflies (Odonata) along streams running through commercial forestry. Odonatologica 29: 195-208.
Kitching, R.L., 2000. Food webs and container habitats: the natural history and ecology of phytotelmata. Cambridge University Press, Cambridge, UK.
Kitching, R.L. & A.G. Orr, 1996. The foodweb from water-filled treeholes in Kuala Belalong, Brunei. Raffles Bulletin of Zoology 44: 405-413.
Korkeamäki, E. & J. Suhonen, 2002. Distribution and habitat specialization of species affect local extinction in dragonfly Odonata populations. Ecography 25: 459-465.
Legrand, J. & G. Couturier, 1985. Les odonates de la forêt de Tai (Côte d'Ivoire). Premières approches: faunistique, répartition écologique et association d'espèces. Revue d'Hydrobiologie Tropicale 18: 133-158.
Lieftinck, M.A., 1942. The dragonflies (Odonata) of New Guinea and neighbouring islands. Part VI. Results of the Third Archbold Expedition 1938-'39 and the Le Roux Expedition 1939 to Netherlands New Guinea (I. Anisoptera). Treubia 18: 441-608.
Lieftinck, M.A., 1949. The dragonflies (Odonata) of New Guinea and neighbouring islands. Part VII. Results of the Third Archbold Expedition 1938-'39 and the Le Roux Expedition 1939 to Netherlands New Guinea (I. Zygoptera). Nova Guinea (N.S.) 5: 1-271.
Lieftinck, M.A., 1976. The dragonflies (Odonata) of New-Caledonia and the Loyalty Islands, Part 2: Immature Stages. Cahiers ORSTOM Office de la Recherche Scientifique et Technique Outre Mer Serie Hydrobiologie 10: 165-200.

Lounibos, L.P., J.H. Frank, C.E. Machado Allison, P. Ocanto & J.C. Navarro, 1987. Survival, development and predatory effects of mosquito larvae in Venezuelan phytotelmata. Journal of Tropical Ecology 3: 221-242.

Louton, J., J. Gelhaus & R. Bouchard, 1996. The aquatic macrofauna of water-filled bamboo (Poaceae: Bambusoideae: Guadua) internodes in a Peruvian lowland tropical forest. Biotropica 28: 228-242.

Mack, A.L., 1998. A biological assessment of the Lakekamu Basin, Papua New Guinea. Conservation International, Washington, D.C.

McGarigal, K., S. Cushman & S. Stafford, 2000. Multivariate statistics for wildlife and ecology research. Springer, New York.

Norusis, M.J., 2000. SPSS professional statistics. SPSS Inc., Chicago.

Novelo Gutierrez, R., O. Canul Gonzalez & J. Camal Mex, 1988. The Odonata from the State of Quintana Roo, Mexico (Insecta: Odonata). Folia Entomologica Mexicana: 13-68.

Ormerod, S.J. & R.W. Edwards, 1987. The ordination and classification of macroinvertebrate assemblages in the catchment of the river Wye in relation to environmental factors. Freshwater Biology 17: 533-546.

Orr, A.G., 2001. An annotated checklist of the Odonata of Brunei with ecological notes and descriptions of hitherto unknown males and larvae. International Journal of Odonatology 4: 135-188.

Orr, A.G., 2003. Dragonflies of Borneo. Natural History Publications, Kota Kinabalu, Indonesia.

Orr, A.G., 2004. Critical species of Odonata in Malaysia, Indonesia, Singapore, and Brunei. International Journal of Odonatology 7: 371-384.

Osborn, R. & M.J. Samways, 1996. Determinants of adult dragonfly assemblage patterns at new ponds in South Africa. Odonatologica 25: 49-58.

Painter, D., 1999. Macroinvertebrate distributions and the conservation value of aquatic Coleoptera, Mollusca and Odonata in the ditches of traditionally managed and grazing fen at Wicken Fen, UK. Journal of Applied Ecology 36: 33.

Paulson, D.R., 2002. Odonata records from Nayarit and Sinaloa, Mexico, with comments on natural history and biogeography. Odonatologica 31: 359-370.

Polhemus, D.A., 1995. A preliminary biodiversity survey of aquatic heteroptera and other aquatic insect groups in the Kikori River Basin, Papua New Guinea. In: WWF (ed.) "Field survey of biodiversity in the Kikori River Basin, Papua New Guinea", World Wildlife Fund, Washington, D. C., pp. 33-47.

Ramírez, A., D.R. Paulson & C. Esquivel, 2000. Odonata of Costa Rica: diversity and checklist of species. Revista de Biologia Tropical 48: 247-254.

Rowe, R.J., 2004. Conservation of Odonata in the South Pacific and Australasia. International Journal of Odonatology 7: 139-147.

Samways, M.J., 1989. Taxon turnover in Odonata across a 3000 m altitudinal gradient in Southern Africa. Odonatologica 18: 263-274.

Schindler, M., C. Fesl & A. Chovanec, 2003. Dragonfly associations (Insecta: Odonata) in relation to habitat variables: a multivariate approach. Hydrobiologia 497: 169-180.

Schridde, P. & F. Suhling, 1994. Larval dragonfly communities in different habitats of a Mediterranean running water system. Advances in Odonatology 6: 86-100.

Stewart, D.A.B. & M.J. Samways, 1998. Conserving dragonfly (Odonata) assemblages relative to river dynamics in an African savanna game reserve. Conservation Biology 12: 683-692.

Stoks, R. & M.A. McPeek, 2003. Antipredator behavior and physiology determine *Lestes* species turnover along the pond-permanence gradient. Ecology 84: 3327-3338.

ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

ter Braak, C.J.F. & P. Smilauer, 2002. Canoco for Windows Version 4.5. Biometris – Plant Research International, Wageningen, The Netherlands.

Timm, H., M. Ivask & T. Möls, 2001. Response of macroinvertebrates and water quality to long-term decrease in organic pollution in some Estonian streams during 1990-1998. Hydrobiologia 464: 153-164.

Vick, G.S., 1999. A checklist of the dragonflies of the South West Province of Cameroon with a description of a new species of the genus *Phyllogomphus* Selys, 1854. Odonatologica 28: 219-256.

Vick, G.S., 2002. Preliminary biodiversity assessment of the odonate fauna of the Takamanda Forest Reserve, Cameroon. IDF-Report 4: 1-10.

Watanabe, M., H. Matsuoka & M. Taguchi, 2004. Habitat selection and population parameters of *Sympetrum infuscatum* (Selys) during sexual mature stages in a cool temperate zone of Japan (Anisoptera: Libellulidae). Odonatologica 33: 169-179.

Watson, J.A.L. & A.L. Dyce, 1978. The larval habitat of *Podopteryx selysi* (Odonata: Megapodagrionidae). Journal of the Australian Entomological Society 17: 361-362.

Watson, J.A.L., A.H. Arthington & D.L. Conrick, 1982. Effect of sewage effluent on dragon-flies of Bulimba Creek, Brisbane. Australian Journal of Marine and Freshwater Research 33: 517-528.

Watson, J.A.L., G. Theischinger & H.M. Abbey, 1991. The Australian dragonflies, a guide to the identification, distributions and habitats of Australian Odonata. CSIRO, Canberra.

Willott, S.J., D.C. Lim, S.G. Compton & S.L. Sutton, 2000. Effects of selective logging on the butterflies of a Bornean rainforest. Conservation Biology 14: 1055-1065.

Wright, D., H.J. Jessen, P. Burke & H.G. de Silva Garza, 1997. Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. Biotropica 29: 250-260.

Yanoviak, S.P., 2001. Predation, resource availability, and community structure in Neotropical water-filled tree holes. Oecologia 126: 125-133.

Yule, C.M., 1996. Trophic relationships and food webs of the benthic invertebrate fauna of two aseasonal tropical streams on Bougainville Island, Papua New Guinea. Journal of Tropical Ecology 12: 517-534.